In the spider nursery: indifference, cooperation or antagonism?

Susan E. Riechert[1], Jonathan Pruitt[2] and Jennifer Bosco[1]:   [1]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville TN 37996-1610, USA; E-mail: riechert@utk.edu; [2]Department of Ecology, Evolution and Marine Biology, University California-Santa Barbara, Santa Barbara, CA 93160, USA

Abstract.   Based on studies of adult behavior, the desert spider *Agelenopsis aperta* (Gertsch, 1934) is considered exemplary of a species exhibiting an aggressive syndrome. This study offers a first examination of the nature of interactions that juvenile *A. aperta* engage in during the period when sibs are clustered on a group web. We test the hypothesis that early instar *A. aperta* lack the aggressiveness noted for older instars. Our data set is comprised of observations of five weekly feedings offered to 818 sibling pairs, constituting an average of 4.6 replicate sib pairs from each of 174 families. At each weekly feeding, a worker termite was offered to each sib in the shared container in which they had built web retreats. We observed no cooperative foraging during the course of these feedings. Rather, most families exhibited a mix of independent foraging and non-injurious contests over prey. We present a brief overview of the occurrence and initiation of contests over prey, with particular reference to the weekly feeding in which contests first occur versus the feeding in which a seminal contest takes place (i.e., where sibs earn permanent winner versus loser status).

Keywords: *Agelenopsis aperta*, sibling interactions, feeding bouts

In arthropods such as spiders, there is a gregarious phase in the life cycle when the young are clustered in the confined space of a silk nest or web. During this period, indirect fitness effects among sibs are likely to occur, in which the behavior of an individual not only influences its own future reproductive success but that of its sibs as well. For example, cooperation in prey capture not only offers positive benefits to sibs that engage in the capture of a prey item, but also to sibs that participate only in feeding on that prey (e.g., *Amaurobius ferox* (Walckenaer, 1830) (Kim et al. 2005). Alternatively, negative indirect effects are expected when resources available to clustered sibs are limited. Both exploitative (independent foraging for prey) and interference competition (agonistic interactions over prey) may produce these indirect negative fitness effects (Keddy 1989).

In this study, we examine sibling interactions of early instar *Agelenopsis aperta* (Gertsch, 1934) during the gregarious phase in the life cycle that takes place in the absence of the mother. *Agelenopsis aperta* is a desert species, which is known for the competitive behavior it exhibits over websites as late instars and adults (e.g., Riechert 1981). Our focal question is whether the agonistic behavior that later instars exhibit towards conspecifics is exhibited at this early stage in the life cycle when cooperative behavior or independent feeding might be favored.

We, thus, examined sib-sib pair behavior during five weekly feedings to establish whether early instars of this species exhibit resource exploitation (independent foraging), contest competition (agonistic interactions over prey), cooperation (joint capture and feeding) or some combination of these three resource utilization strategies. The nature of contest initiation is additionally outlined herein.

METHODS

Test system.—*Agelenopsis aperta* is an arid-lands spider that occupies the full range of habitat types found at elevations below 1800 m in the southwestern United States and Mexico. This species' web is comprised of a non-sticky sheet upon which prey capture and agonistic interactions occur. There is also a silk-lined funnel retreat that leads into a protected area, such as a crevice or under a rock or stump. Extensive work by Riechert and colleagues over the past forty years has led to a wealth of information regarding the ecology and behavior of this species as well as the role of population ecology in behavioral differentiation (See reviews in Riechert 1993, 1999, Riechert et al. 2001).

As spiderlings emerge from the egg case they lay down silk, forming a communal web. Individuals produce silk retreats within this web structure and begin feeding on prey within 10 days of emergence (Riechert, personal observations). This communal web is occupied for several weeks. As individuals begin dispersing from it, they build individual webs nearby (Riechert 1974). The high density of siblings through the first month following emergence from the egg case offers the opportunity for cooperative foraging as well as for agonistic encounters over prey. This forms the impetus for our study of *A. aperta* interactions at this stage of the life cycle.

Collection and pair establishment.—Gravid females from two arid west Texas locations—a mesquite-dominated flat just west of the town Balmorhea in Reeves County (30.97°N, 103.75°W) and a cactus scrub hillside just east of the Big Bend National Park in Brewster County, TX (29.32°N 103.14°W)—provided the source of F2 offspring of 174 F1 generation females. As we found no size biases among spiderlings within a clutch (Fisher Scientific accu-124D balance mass determinations), we randomly assigned sibs from each family to pairs. The number of replicates initially established depended on clutch size, with a maximum of ten pairs from any one family. We marked each sib in a pair with fluorescent powder of a different color before releasing them into a plastic container measuring 3.5 cm in dia and 1 cm in height. We refurbished the respective color markings as necessitated by molts.

Weekly staged feedings.—At each of five weekly feedings, we simultaneously dropped a worker termite (*Reticulitermes flavipes* (Kollar,1837)) at the funnel entrances of the two sibs sharing a container. (Note that one termite is approximately three times the mass of an early instar *A. aperta* (Mean termite

mass = 1.89 ± 0.03 mg; mean *A. aperta* spiderling mass = 0.54 ± 0.01mg). Subsequently, we scored the behavior of the sibs for a five-min period or until prey capture activities had ended. We revisited each sib pair ∼30mins later to record the feeding status of each sib (i.e., did the respective sibs each have a termite secured at its web funnel, were both sibs feeding on the same termite, or did one sib have control of both termites introduced into the shared container?).

A contest over prey in a particular weekly feeding was declared "seminal" when it led to a clear resolution of each individual's competitive status relative to its sib for that and all subsequent weekly feeding bouts. In this study, there were two potential contest outcomes. Competitive interactions could end in a "draw" or with the identification of a distinct contest "winner" and "loser". The outcome "draw" leads to subsequent independent foraging by the paired sibs. (Each sib attacks and feeds only on the termite offered to it at its funnel entrance, without respect to what its sib is doing.) On the other hand, "winners" of seminal contests tend to monopolize future prey offerings, while "losers" defer to their winning sib in subsequent feeding opportunities. The winner/loser seminal contest outcome can lead to marked differences in the growth rates of the paired sibs, particularly when contest resolution occurs early in the series of five weekly feedings (a topic of a later paper on this system).

Analyses.—Our final data set consisted of 818 surviving sib pairs with a mean number of 4.6+ 0.04 replicates/family and a total of 4,090 feeding bouts. We used the statistical package JMP® Pro version 12.0 (SAS Institute Inc) in the completion of these analyses. Chi square tests were applied to simple frequency questions and logistic regression applied in examining the potential influences of family and population on juvenile behavioral type representation.

RESULTS

Satiation prey levels.—Our test for the assumption that a single termite prey offers food greater than what an early instar *A. aperta* can consume is substantiated by 162 observations of different individuals feeding on a termite offered the previous week. No significant relationship exists between an individual's size relative to its sib and its propensity to feed on an old prey item ($X^2_2 = 0.79$, $P = 0.37$, $n = 162$). Further, feeding on a prey item remaining from past feedings occurs randomly across the five weekly feedings ($X^2_3 = 7.04$, $P = 0.07$).

Foraging strategy representation.—Sixty-five percent of sib pairs engaged in contest competition during at least one weekly feeding trial. Thirty-five percent of sibling pairs never engaged in contest competition and demonstrated only independent foraging. None of the sibling pairs demonstrated cooperative foraging. The significant whole model test result ($X^2_{165.816} = 264.67$, $P < 0.001$) reflects a significant family effect only. No significant population (collection locality) effect is present ($X^2 = 0.12$, $P = 0.72$). Inspection of the data indicates that most families exhibit some mix of sibs that forage only independently and those that contest prey in the paired sib context. We did find, however, that all sib pairs contested prey at least once in 24.5% of the families, while all sib pairs foraged independently in another 5% of the families (Fig. 1).
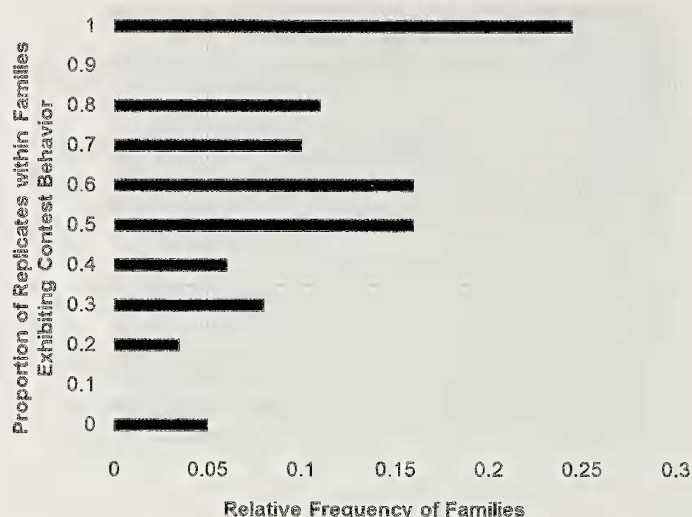

Figure 1.—Family distribution of proportions of replicate sib pairs exhibiting contest competition during at least one feeding bout during the 5 weeks of the experiment.

Contests over prey.—Contests between sibs over prey offered in a weekly feeding occur when an individual ignores (78.2%, n = 471) or abandons (21.8%, n = 131) the termite offered at its own funnel entrance, and encroaches on the termite offered to its sib. A total of 531 of the 818 sibling pairs demonstrated contest competition in at least one of the five weekly feedings. The average number of weekly feedings in which a pair of sibs contested prey equaled 1.52 + 0.04, and only 3% of sib pairs engaged in contests over prey in more than three of the five weekly feedings (Table1). Although there was a familial effect on *whether or not* sibs contested prey in at least one of the weekly feedings (Fig. 1), no familial effect was found in the *number* of weekly feedings in which sib pairs contested prey ($F_{ratio} = 1.08$, P = .47).

Table 1 presents data on the timing of contests over prey over the course of the five weeks of the experiment. Table 1(A) shows the proportion of all contest events, sib-pairs' first contest events and sib-pairs' seminal contests (establishing ultimate winner/loser status) that took place during each of the five weekly feedings.

Table 1(B) presents summary statistics for three categories of contests experienced by sib pairs (all contests, first contest and seminal contest). Mean first contest is the average of the week numbers (1 through 5) in which sib pairs experienced their first contest over prey. Mean seminal contest is the average of the week numbers in which each sib pair experienced a contest that established a winner and loser in that contest and all subsequent contests. Mean for all contests indicates the average week number in which any contest over prey took place.

Although first contests may prove to be seminal contests, on average the seminal contest occurs after the first contest. The timing of first contests (mean week = 2.13 ± .06) and seminal contests (mean week = 2.67 ± .06) over the five weekly feedings differ significantly ($X^2 = 45.1$, P <0.00001). Standard errors are measures of the accuracy with which a sample represents a "population". The small standard errors reflect the large sample sizes (number of sib pairs) and thus, high

Table 1.—Timing of sib-sib contests over prey, over five weekly feedings. (A) Distribution of three types of contest events across five weekly feedings. Each sib pair can experience one "first contest" and no more than one seminal contest (see text); a first contest may prove to be a seminal contest. "Total contests" refers to all contests (first, seminal or other) a sib pair engages in over the course of five weekly feedings. Figures indicate the proportion of each type of contest event (first, seminal or total contests) that occurred during each weekly feeding period. (B) Summary statistics. Means are calculated as the average weekly feeding period (1 through 5) in which each sib pair experienced any contest over prey, in which each sib pair's first contest occurred, and in which a seminal contest occurred. The low standard error values reflect the fact that the mean parameter estimates are accurate indicators of the true weekly distribution of the respective contest types.

A. Weekly Feeding	Proportion of total contests	Proportion of all 1st contests	Proportion of all seminal contests
1ST	0.621	0.44	0.28
2ND	0.283	0.26	0.23
3RD	0.064	0.13	0.20
4TH	0.016	0.09	0.15
5TH	0.016	0.08	0.14
B. Summary Statistics	All contests	1st contests	Seminal contests
Mean week in which sib groups experienced contests of each type	1.52	2.13	2.67
Standard Error	0.04	0.06	0.06
Sample Size (# sib pairs)	531	531	529*

* Two contests unresolved during course of five weekly feedings.

accuracy of the mean estimates provided for the three aspects of contest timing with respect to the five weekly feedings.

Note that only two of the 531 sib pairs followed in this study failed to establish draw/winner/loser status over the course of the five weekly feedings. Further, there were only 24 contests that ended in a draw, with individuals subsequently foraging independently. Thus, the vast majority of the seminal contests (95.1%) led to distinct winner/loser designations for the paired sibs.

Contest-initiating acts can be broadly differentiated as being prey-directed versus sib-directed. Prey-directed actions consist of joining in the capture of a termite that has been offered to its sib or carrying off a termite that has already been secured by its sib. These prey takeovers account cumulatively for only 27% of the behavioral acts that initiate sib-sib contests over prey. The majority of the contest initiating acts are sib-directed such as blocking the sib from reaching its prey item and shoving or chasing it away from it. Chase sib from its prey (33%) and lunge at sib (25%) are prominent sib directed contest initiating acts. The distribution of behavioral acts sibs engage in differs significantly between 1st interactions and seminal interactions ($X^2 = 20.95$, P <0.001, df = 9). (Note that 1st interactions that are also seminal interactions were excluded from this analysis.) First interaction deviations from expectations contributed most to the significant test result. This included lower than expected incidences of the initial act involving prey take away, blocking sib from/shoving sib off prey, threats directed towards sib, hovering by a sib in possession of a termite and following of the sib with bumping

of it. On the other hand, there was more sib following, sib chase away from prey and grappling between sibs as the interaction initiating behavior in 1st interactions than expected.

DISCUSSION

Foraging strategy representation.—We argue that our experiment is biased towards cooperative foraging over independent foraging and competition. This is because a worker termite is ~three times the mass of an early instar *A. aperta*. It takes much silk investment to secure a worker termite, which also offers more mass than can be consumed in a feeding bout. Nevertheless, no sib pairs were observed to share in the capture and feeding on a termite in this study. This result is indicative of early (constitutional) determination of behavioral temperament.

While we did not observe any instances of cooperative foraging, we did detect significant levels of both familial and within clutch variation in behavioral tendencies of early instar *A. aperta*. The phenotype mix (24.5% of the families at the aggressive end and 5% at the passive end of a continuum in behavioral temperament) is potentially reflective of the meta-population structure of *A. aperta* in the desert southwest US. Here small patches of riparian habitat are interspersed within an arid-land habitat matrix with much gene flow particularly from arid adapted into riparian local populations (Riechert et al., 2001). Low aggressiveness is the prominent phenotype in riparian habitats offering abundant prey, but also where predation pressure by birds is quite high (e.g., Hammerstein & Riechert 1988; Riechert & Hall 2000). High aggressiveness is the prominent phenotype in more arid areas, reflecting competition for web sites offering both maximum foraging time and prey capture success with encountered insect prey (Riechert & Tracy 1975; Riechert 1976).

Fitness implications.—Contest competition is, in a sense, a "bet hedge" against harsh environments. Under conditions with limited resources, scramble competition (independent foraging) is more likely to lead to volatile boom-and-bust population dynamics and population die-offs (after Hassell 1975; Lomnicki 2009). Contest competition, in contrast, allows winners/dominants to emerge and potentially reach the body size thresholds required to reproduce (Sharpe & Avilés 2016). Given the harsh arid environmental conditions typically experienced by *A. aperta*, and the expected indirect fitness benefits of insuring the survival of some individuals within a family, contest competition might well be expected to prevail in sib-sib interactions during the aggregative phase of the life cycle. It provides insurance that the better competitors within a family gain contest experience and potential greater access to prey during times when food is limiting. Full treatment of contest structure and the fitness consequences of contesting prey at this stage of the life cycle is beyond the scope of this short conference proceedings and will be presented elsewhere.

ACKNOWLEDGMENTS

LITERATURE CITED

Hammerstein, P. & S.E. Riechert. 1988. Payoffs and strategies in spider territorial contests: ESS-analyses of two ecotypes. Evolutionary Ecology 2:115–138.

Hassell, M.P. 1975. Density-dependence in single-species populations. Journal of Animal Ecology 44:283–295.

Keddy, P.A. 1989. Competition. Chapman and Hall, London.

Kim, K.W., B. Krafft & J.C. Choe. 2005. Cooperative prey capture by young subsocial spiders. Behavioral Ecology and Sociobiology 59:92–100.

Lomnicki, A. 2009. Scramble and contest competition, unequal resource allocation, and resource monopolization as determinants of population dynamics. Evolutionary Ecology Research 11:371–380.

Riechert, S.E. 1974. The pattern of local web distribution in a desert spider: mechanisms and seasonal variation. Journal of Animal Ecology 43:733–746.

Riechert, S.E. 1976. Web-site selection in a desert spider, *Agelenopsis aperta* (Gertsch). Oikos 27:311–313.

Riechert, S.E. 1981. The consequences of being territorial: spiders, a case study. American Naturalist 117:871–892.

Riechert, S.E. 1993. The evolution of behavioral phenotypes: lessons learned from divergent spider populations. Advances in Animal Behaviour 22:103–134.

Riechert, S.E. 1999. The use of behavioral ecotypes in the study of evolutionary processes. Pp. 3–32. *In* Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms. (S. Foster, J. Endler, ed.). Oxford University Press, U.K.

Riechert, S.E. & R.F. Hall. 2000. Local population success in heterogeneous habitats: reciprocal transplant experiments completed on a desert spider. Journal of Evolutionary Biology 13:1–10.

Riechert, S.E. & C.R. Tracy. 1975. Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. Ecology 56:265–284.

Riechert, S.E., F.D. Singer & T.C. Jones. 2001. High gene flow levels lead to gamete wastage in a desert spider system. Genetica 112/113:297–319.

Sharpe, R.V. & L. Avilés. 2016. Prey size and scramble vs. contest competition in a social spider: implications for population dynamics. Journal of Animal Ecology 85:1401–1410.